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Subtle behavioral variation in wild chimpanzees, with special reference to Imanishi's concept of *kaluchua*.

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Abstract

Here we consider the concept of *kaluchua* (a word adopted from the English "culture") in group-living animals developed by Imanishi in the 1950s. He distinguished it from *bunka* (the Japanese equivalent to the English "culture") because he thought that *bunka* had strong connotations of noble and intellectual human-like activities. Although he did not rigidly define *kaluchua*, his original concept of *kaluchua* was much broader than *bunka* and represented non-hereditary, acquired behavior that was acknowledged socially. However, instead of social life, complex feeding skills have often formed the central topic in the current studies of animal culture. In order to provide evidence that more subtle behavioral variations exist among wild chimpanzee (*Pan troglodytes*) populations, we directly compared the behaviors of two well-habituated chimpanzee groups, at Bossou and Mahale. During a 2month stay at Bossou, M.N. (the first author) saw several behavioral patterns that were absent or rare at Mahale. Two of them, "mutual genital touch" and "heel tap" were probably customary for mature females and for mature males, respectively. "Index to palm" and "sputter" are still open to question. These subtle patterns occurred more often than tool use during the study period, suggesting that rarity is not the main reason for their being ignored. Unlike tool use, some cultural behavioral patterns do not seem to require complex skills or intellectual processes, and sometimes it is hard to explain the existence of such behaviors only in terms of function.

Keywords: Bossou, Culture, Mahale, Pan troglodytes, Kinji Imanishi

Introduction

Many researchers interested in culture in non-human animals, both from the West and the East, acknowledge that Imanishi (1952) introduced the idea of culture to early primatology even before the discovery of the famous sweet-potato washing by Koshima monkeys (Kawamura 1959). In a Japanese essay, an evolutionist (Imanishi), a human (layman), a monkey, and a wasp discuss the evolution of humanity. Many authors have cited this essay in English articles (Kawamura 1959; Itani and Nishimura 1973; Nishida 1987, 2003; de Waal 1999, 2001; Hirata et al. 2001), but Imanishi did not simply apply culture to non-human animals in the sense that we use the term for humans, he coined a new term, *kaluchua*. *Kaluchua* is a word adopted from the English "culture", and he used it instead of the word *bunka*, the usual Japanese equivalent of culture.

In Imanishi's (1952) essay, when the evolutionist first begins to introduce the concept of *kaluchua*, the human jumps to a conclusion, saying that "Certainly, we became human, not animals, because we had *bunka*". This was probably a widely accepted view at the time, that only humans had *bunka* (culture). But the evolutionist interrupted by saying, "Wait a minute. I did not say *bunka*, I said *kaluchua*." Then he continued introducing his concept of *kaluchua*. It is difficult to translate this part accurately into English, because both *bunka* and *kaluchua* can be translated as culture. Thus, those who have cited the essay have omitted the part in which Imanishi differentiated *kaluchua* from *bunka*.

How did Imanishi differentiate these two terms? Unfortunately, Imanishi did not rigidly define *kaluchua*. He said that *kaluchua* was much broader than *bunka* and was non-hereditary, acquired behavior that was acknowledged socially; consequently its existence inevitably requires continuous group-living. Later, when Imanishi (1966) stopped using this special term, he explained why he had been using the term *kaluchua* and avoiding the term *bunka*: it was because the nuance of the term *bunka* was human-centered and it recalled something like "an ape wearing a costume". The term *bunka* connoted somehow noble, intentional, sophisticated, and complex aspects of our intellectual activities, at least in his time. It may be for the same reason that Kawamura (1959) used the term "sub-culture", and Kawai (1965) used "pre-culture" in their English papers (both used *kaluchua* in their Japanese writings; Kawamura 1956; Kawai 1963). Although some Japanese researchers, such as Itani (1981, 1991), continued to use the term *kaluchua*, many Japanese primatologists

now usually employ the term *bunka* in their Japanese writings (e.g., Nishida 1980a; Kuroda 1999; Sugiyama 2000; Matsuzawa 2001a; Nakamura 2003a).

Following Imanishi's prediction of *kaluchua* in group-living animals, many studies were done on Japanese monkeys (as summarized in Itani and Nishimura 1973). At that time, the concept of *kaluchua* was much broader (e.g., Kawamura 1956, 1965; see also Mizuhara 1986 for criticism of such a pan-*kaluchural* approach). But as the sweet-potato washing by Koshima monkeys (Kawamura 1959; Kawai 1965) became famous and almost emblematic of monkey culture, Imanishi (1966) once commented bitterly that sweet-potato washing was only a peripheral phenomenon in his *kaluchua* concept. Following this line, Itani (1991) wrote that "Frankly speaking, I think the concept of *kaluchua* by Imanishi has been impoverished and its remainder has been restricted to very limited areas of 'knowledge and the techniques for subsistence'..... The domains of social behaviors or social organizations have seldom been stated in terms of *kaluchua*". Here, by "knowledge and the techniques for subsistence", he may have had the foraging tool use of chimpanzees (*Pan troglodytes*) in mind. Tool use or potato washing is something very human-like because they seem to be complex and sophisticated for mere animals. Such behavior can easily be attributed to *kaluchua* (or *bunka*, culture, whatever). What Imanishi and Itani wanted to stress were aspects of *kaluchua* as the means of group-living. For example, Imanishi (1952) wrote "A group does not split into individuals because of *kaluchua*" and Itani (1957) wrote "It can be said that *kaluchural* personality is what makes mutual communication possible and makes bonding between individuals to form an orderly group". For them, *kaluchua* was not restricted to complex feeding skills or techniques. Rather, their question was whether group-living could be explained in terms of *kaluchua* and if something of social organization was inherited through *kaluchua*. For Imanishi, and perhaps for Itani also, *kaluchua* is something maintained by "identification" (Imanishi 1957).

Although we are not calling for the revival of the special term coined by the late Japanese primatologist (thus, hereafter, we mainly use the term "culture"), since labels are less important than content (McGrew 2004), we think that Imanishi's original idea is still worth investigating and developing further. It may still be premature to deal directly with social organization or group-living from the standpoint of primate culture, but we would like to approach the issue from the side of culture that may have been obscured by the conspicuousness of various types of tool use.

Chimpanzees have subtle social customs and other behavioral variations that are simple in terms of their motor patterns, but the function of such behavior is sometimes difficult to grasp. Such behavior patterns have sometimes been seen and recognized by researchers, but not well-described or discussed in terms of chimpanzee culture, perhaps because of their subtlety and/or casualness. For example, neither grooming hand-clasp (McGrew and Tutin 1978) nor social scratch (Nakamura et al. 2000) had been considered social customs until researchers from Gombe (McGrew and Tutin in the former case, Marchant and McGrew in the latter) visited Mahale. This does not mean that these behavior patterns were new to the Mahale researchers. Rather, patterns had been included in the larger category of social grooming, as they always occurred in the context of grooming. For Mahale researchers, these were familiar and casual behaviors, but they had never considered that they might be absent in other populations because they had no opportunity of observing a group of chimpanzees other than those in Mahale.

Methods

Subtle social behavior patterns are unlikely to be recognized as social customs since ethologists usually observe only one group of chimpanzees. The recognition of grooming hand-clasp and social scratch as social customs by "fresh eyes" suggested a new method of studying chimpanzee cultures. We launched a "culture hunting" in 2000. We mean by "culture hunting" that researchers familiar with behavior patterns of one local population visit other populations, take detailed video images of their behavior, and compare the behavioral patterns between the two. Thus, in 2001, T.N. (the second author) visited the Kibale Forest, Uganda. Within 4 weeks of the study, he found that not only the social scratch pattern but also grooming sounds of the Ngogo chimpanzees differed from those of their Mahale counterparts (Nishida et al. 2004). In 2002, Shimada (2003) visited Gombe briefly and also found something different from the social scratch patterns of Mahale.

Here, we present some examples of subtle behavioral variations by direct comparison between Bossou and Mahale. M.N. visited Bossou from mid-January to mid-March 2003 and followed four males and five females for a total of 241 h. Filming on digital videotape or dictating onto cassette tape, he recorded the behavior of target individuals and of those close (ca 5–10 m) to the targets. He especially looked for patterns that are absent or unfamiliar at Mahale, and eventually found some. Afterwards, T.N. confirmed whether the patterns were present or absent at Mahale. Both authors are well accustomed to the behavior patterns of Mahale chimpanzees, as M.N. has studied Mahale chimpanzees, focusing mostly on social behavior (Nakamura 2000, 2003b), for an accumulated total of more than 2 years and T.N. has studied them for 11 years.

Bossou is in southeastern Republic of Guinea, and the western subspecies of chimpanzees (*P. t. verus*) has been the subject of research (Sugiyama and Koman 1979a). For more than two decades, there has been little fluctuation in the group size (Sugiyama 1999), which was 19 (including infants) when M.N. visited there. Mahale (Nishida 1990; Nishida et al. 2002) is in the western Republic of Tanzania, and the eastern subspecies of chimpanzees (*P. t. schweinfurthii*) lives there. Group size has been 3–4 times larger (Nishida et al. 2003) than that of Bossou, and was 60 (including infants) at the end of 2004.

Table 1 summarizes some of the reported behavioral variations between Bossou and Mahale. Various types of foraging tool use have been reported from Bossou, whereas only arboreal ant fishing is the customary for-

aging tool use at Mahale. Thus Bossou chimpanzees are highly "technological" compared with Mahale chimpanzees, so if we talk only about the material aspects, Bossou is more cultural than Mahale. In contrast, if we look at behavioral patterns other than foraging tool use, many fewer have been reported from Bossou. In particular, few behavior patterns in social contexts have been reported as culture at Bossou.

Results

Observations at Bossou

Mutual genital touch

When two adult females at Bossou met each other after some time apart, they approached to and then passed by each other closely. They paused with one's face close to the other's hip. Then they simultaneously and gently touched each other's genital area from underneath with the outer hand (Fig. 1). In about half of the cases observed, only one individual touched the other's genitals, although both took the same posture. Mutual genital touch may seem similar to genital inspection, as often performed by male chimpanzees, but is different because the females did not touch the vaginal opening nor sniff their finger in this behavior. The genital inspection seen among adult males of Mahale was also done many times by Bossou males (Nakamura, personal observation). Mutual genital touch may be a kind of greeting between females, as its context was similar to peering into the face, kissing, or extending a hand. Usually no vocalizations were heard, but there were a few cases in which faint, soft grunts were given by one party. Mutual genital touch was done by seven of nine sexually mature females (done by Fn, Jr, Ka, Nn, Pm, Yo, and Vv; not by Vl and Ft). Note that two 9-year-old females, Vv and Ft, were included as mature females because they had already given birth. This behavioral pattern has not been seen at Mahale.

Heel tap

This behavioral pattern at Bossou was described by Sugiyama (1989) as "knock branch with heel," but it has

not appeared in later studies of chimpanzee culture (e.g., Whiten et al. 1999). In this pattern, a tree bough, rock, or the ground was rhythmically tapped with the heel (Fig. 2). This was not the usual stamping, because the sole made no contact with the substrate, but instead the sole stayed upright facing forward and only the heel made contact. When the heel was tapped against a bough, a conspicuous sound was produced. At Mahale, stamping is common but heel tapping does not occur.

Heel tap was done by three of the four sexually mature (adolescent and adult) males (done by TA, FF, and PO; not by YL). With one exception by a juvenile male, JJ, all M.N.'s observations belong to these three mature males (although about half of the cases reported by Sugiyama (1989) were by juveniles). Adult females were never seen to heel-tap, either in this study or in Sugiyama's (1989). In M.N.'s observations, 53 out of 56 cases were considered part of courtship displays (because it was directed to an estrous female nearby), especially when soliciting an estrous female for consorting, and the behavior was often used jointly with branch shaking, stamping, or leaf-clipping. In only three cases (one by the juvenile male, JJ, and two by an adolescent male, PO), were the contexts not sexual courtship, and, as Sugiyama (1989) suggested, this behavioral pattern may also be used for inviting play. All three mature males who heel-tapped lateralized it to one or the other of their feet. Two older males (FF and TA) always used the left foot and the other young male (PO) used the right foot whenever they heel-tapped (n=7, 32, 15, respectively). In the 23 cases in which the behavior was videotaped clearly enough, they tapped 5.5 times on average (SD=3.9, range: 2–20) per bout.

Index to palm

This behavioral pattern always occurred during social or self grooming. In social grooming, the groomer suddenly stopped grooming, often turning his back on the groomee. His lips moved continuously, as if something was held between the lips. Next, he opened his palm and placed a small particle on the palm from his lower lip, and then he put his index finger on the spot, poking, pushing and dragging the item (Fig. 3). Finally, he again put his mouth to the palm, presumably to eat the particle. Other individuals, especially infants and juveniles, sometimes peered into the palm, although the frequency of this was not recorded systematically. This pattern was observed for three mature males (TA, FF, and PO) and two mature females (Pm and Ft).

This behavioral pattern may be comparable to leaf grooming at Mahale, as leaf grooming is not seen at Bossou and the contexts are similar. At Mahale, Zamma (2002) found that a louse was attached to a leaf that had been being used for leaf grooming and abandoned, implying that the function of this pattern may be to squash a parasite. At Taï, Boesch (1996) reported that the same function was achieved by a behavior called "index hit". Index hit at Taï is similar to this pattern at Bossou, but different because the ectoparasite is put on one's forearm in index hit, instead of the palm. Although it has not yet been confirmed at Bossou, it is likely that the particle put on the palm was also an ectoparasite captured during grooming.

Sputter

According to Nishida et al. (2004), Ngogo chimpanzees during grooming make a sputtering sound, which is completely absent at Mahale. M.N. heard the same kind of sound from three individuals (JJ, Ft, and PO) at Bossou. This sounded as if the chimpanzees forced air through their lips. Compared to Ngogo where 27 individuals were confirmed to utter this sound (Nishida et al. 2004), it seems to be limited to a much smaller number of individuals at Bossou, the juvenile male JJ performing 20 of the 24 cases observed. Further investigation is needed to see whether more individuals perform this.

Other behaviors to note

Here, we note some other behaviors of Bossou chimpanzees that are rare or absent at Mahale. Although it may not be appropriate to mention these behaviors in

our cultural context, there at least seem to be differences between the two sites that promise to yield valuable data if they are investigated further.

The first behavior is anus massage by an adolescent male, PO. He often massaged his anus with one of his fingers while reclining. It may be that he was just feeling itchy because of infection, parasites, or some other reasons, but it looked as if he did so just by habit. This behavior pattern was performed only by one individual, and is thus likely idiosyncratic.

The second one is mother–offspring mating. Of the four sexually mature males at Bossou, three still have living mothers. Two of these sons, FF (23 years old) and YL (11 years old), mated with their mothers three times each during M.N.'s study period. FF and YL were the alpha and the beta males, respectively (Nakamura and Ohashi 2003). FF's copulations were almost forced, as his mother refused and screamed all the time. For YL, his mother presented and copulated just as she did with other males.

The last one is coprophagy. Although it is very rare at Mahale (Nishida et al. 1999), three individuals at Bossou, Ka (an old female) and FF and TA (adult males), ate their feces during this short research period. In a clearly observed case, Ka put feces to her lips, picked several seeds from the feces, and crunched them to eat. Seeds were about 1 cm in the major axis with whitish color; unfortunately, however, the species was not identified. Other observed cases for FF and TA were not as clear as Ka's, but seemed identical to hers. Food scarcity cannot simply explain this behavior because January to March is the high fruiting season (Yamakoshi 1998).

Frequency and number of performers

How do the frequencies of some of these patterns at Bossou compare to that of tool use? (See Table 2.) Heel tap, index to palm, mutual genital touch, and sputter are more often seen than any foraging tool use (ant dip, use of a leaf to drink, nut crack, pestle pound, and use of a stick to get honey), but January to March is the leanest season for tool use (Yamakoshi 1998). Except for leaf-clip, the numbers of performers were too few, probably because of the brief observation time, to evaluate whether these patterns are customary in this group. However, some of the behavioral patterns may be age–sex specific. For example, heel tap was done by three of the four mature males. Similarly, mutual genital touch, presumably a pattern of mature females, was done by seven of nine mature females. This implies that these two types of behavior may be customary, at least to certain age–sex classes.

Index to palm is still open to question, as this behavior was performed only by five individuals, despite its not being limited to a particular age–sex class. However, these few performers was not less than those for any single foraging tool use. Also, index to palm requires the observer to be at a relatively close distance and to have proper angles of observation, e.g., if the chimpanzees are grooming in a high tree or if the groomer is showing only the back, then the observer may be unable to see this behavior (which may be the reason that this pattern has not been recorded until now). Thus, the frequencies are likely to be underestimated, and follow-up observations may show that more individuals do this.

Discussion

The behavioral patterns described above, although absent or rare at Mahale, have not yet been confirmed to be "cultural" in the sense of Whiten et al. (1999). Nor have these behaviors been shown to lead directly to the formation of social structure or the maintenance of a society, as Imanishi and Itani emphasized in the concept of *kaluchua*. However, it is important that only 2 months of observation revealed several subtle behavioral variations between Bossou and Mahale; this again suggests that there is greater behavioral variation in wild chimpanzees than we currently understand. There are several reasons why such behavioral variations have not been recorded, and we argue for the significances of studying such variations.

Tool use has attracted the most attention in the study of chimpanzee cultures. At Bossou, tool use has been the main topic of research, and the same types of tool use have been repeatedly investigated by various researchers from different perspectives (see Matsuzawa and Yamakoshi 1996 for review). This tendency is partly because tool use is important for considering human evolution and the origins of material culture (McGrew 1992). This is similar to the reason why hunting by chimpanzees has also drawn so much attention (e.g., Stanford 1999). Thus, new observations of tool use or hunting by a population of chimpanzees are reported immediately, even when the observations are indirect or based on a few cases (e.g., Hashimoto et al. 2000). In contrast, no one reports a single case of observing a group of chimpanzees greeting each other in a new way. There appear to be biases toward particular topics on the part of observers.

Another reason why researchers are attracted to tool use is that it requires complex object manipulation and some understanding of relationships between or among objects (e.g., Matsuzawa 2001b), for which lengthy learning is essential. In the comparative cognitive sciences, culture sometimes includes in its definition special forms of learning such as imitation and teaching (Tomasello et al. 1993; Byrne et al. 2004)If searching for complex learning capabilities is required in order to assume culture, one is easily directed toward complex behavior such as tool use. Thus, when chimpanzees are experimentally studied to determine whether they are able to imitate (e.g., Whiten 1998), they are usually tested with problems of object manipulation.

Hidden in such conspicuous and complex cultural behavior are more subtle and simple patterns that differ among wild chimpanzee populations. At least during M.N.'s observations at Bossou, the behavior reported in this paper occurred more often than tool use. This suggests that the frequencies cannot simply explain why these patterns have been rarely mentioned in studies of chimpanzee culture. Even when common behavioral patterns are described, researchers are unlikely to imagine them to be absent in other populations. Good

examples are social scratch at Mahale (Nakamura et al. 2000) and heel tap at Bossou. Sugiyama (1989) in first describing the latter suggested that such "expressive behaviors are supposed to be emotional and more or less innate..." and thus "...local differences ... must be little". Since then no one has discussed heel tap in terms of culture.

Another reason that such subtle behaviors remain undescribed is that their functions sometimes cannot be identified, or when they can, the behavioral patterns seem to be arbitrarily related to the functions (Boesch 1995). For example, we still do not know the concrete function of the grooming hand-clasp, or why three different methods, leaf groom, index hit, and index to palm, are employed in different populations of chimpanzees for the same function of squashing parasites. On the other hand, the direct function of tool use is usually easier to discern, and although there is some variation, the way chimpanzees use tools for a certain purpose is straightforward and even predictable from the perspective of efficiency. Within the current framework of behavioral biology that emphasizes adaptation, it is sometimes difficult to describe behaviors when their benefits seem no more than ambiguous (Nakamura 2003a).

What is conspicuous and what is subtle?

We have used the term "subtle" to refer to undescribed or unemphasized local variations in order to contrast them with "conspicuous" and well-documented tool use. But heel tap may be a more conspicuous pattern than some kinds of tool use. What is conspicuous and what is subtle are decided by human observers, and this determination does not necessarily reflect the importance of such behaviors in the life of chimpanzees. It could be that to share the same way of squashing parasites with others may be more important for them than to obtain some amount of food by using a certain type of tool. We do not yet have the answer, but we must not forget that observation is always biased toward what we think is important, which is always a relative judgment.

Significance of subtle behavioral variations

As discussed above, some behavioral patterns may not have received much attention due to the obscurity of their functions or their apparent arbitrariness. We argue that these need to get more attention in studies of animal culture for the same reason. In human culture, there are obviously arbitrary and irrational behavior patterns (e.g., rituals and ways of greeting) upon which cultural anthropologists often focus. We cannot simply assume that chimpanzee "cultural" behavioral patterns are equivalent to those in human culture. However, it is essential to accumulate examples of such subtle behavioral variations in order to see if such behavior patterns are really generated arbitrarily. It may also be important to see if the process of maintaining such patterns in a group lasts for a long time.

Finally, we return to the importance of these subtle variations in relation to the concept of *kaluchua* by Imanishi (1952). We have reconsidered this concept because his interest was not to emphasize complex and sophisticated aspects of culture but to find connections between *kaluchua* and continuous group living (which is more than simple aggregation). He predicted that group-living animals would have *kaluchua* but at the same time argued that *kaluchua* makes group living possible (ibid.). This is a circular argument, but may be an inevitable one. A society and the behavior of individuals or interactions among individuals may not be connected by simple causal relationships. Chimpanzees' everyday social lives are not made up only of conspicuous (to human observers) behavior. There may exist a key to understanding complex and rich relationships within societies, cultures and individuals in the variations of seemingly simple and subtle behaviors.

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Table 1 Behavioral variations at Bossou and Mahale that are relatively well-documented. "○", customary behavior patterns; "+", patterns seen in only a few individuals; "–", absent or not reported

Behavior	Category	Bossou	Mahale	Source[a]
Nut crack	Foraging/tool use	○	–	Sugiyama and Koman 1979b
Pestle-pound	Foraging/tool use	○	–	Yamakoshi and Sugiyama 1995
Leaf for drink	Foraging/tool use	○	+	Sugiyama and Koman 1979b; *Matsusaka and Kutsukake 2002*
Driver ant dip	Foraging/tool use	○	–	Sugiyama et al. 1988
Algae scoop	Foraging/tool use	○	–	Matsuzawa et al. 1996
Termite fish	Foraging/tool use	+	–[b]	Humle 1999
Arboreal ant fish	Foraging/tool use	–	+	*Nishida 1973*
Leaf clip	Social (courtship)/frustration/ tool use	○	○	Sugiyama 1981; *Nishida 1980b*
Throw splash	Social (display)/tool use	–	○	*Nishida 1994*
Shrub bend	Social (courtship)	+[c]	○	Whiten et al. 1999; *Nishida 1997*
Grooming hand-clasp	Social (groom)	–	○	*McGrew and Tutin 1978*
Social scratch	Social (groom)	–	○	*Nakamura et al. 2000*
Leaf groom	Ectoparasite handling/tool use	–	○	*Zamma 2002*
Leaf-pile pull	Solo-play	–	○	*Nishida and Wallauer 2003*

[a] References for Bossou are in roman and for Mahale in italic
[b] No reports for Mahale M group, but reports for Mahale B (Nishida and Uehara 1980; McGrew and Collins 1985) and K (Uehara 1982) groups
[c] M.N. saw only one adolescent male did this pattern

Table 2 Frequency of possible cultural behavioral patterns and tool use at Bossou[a]

	Frequency of events[b]	Number of performers	Names of performers[c]
Heel tap	56 (0.23)	4	TA, FF, PO, JJ
Index to palm	13 (0.05)	5	TA, FF, PO, Pm, Ft
Mutual genital touch	17[d] (0.07)	7[e]	Ka, Nn, Fn, Jr, Pm, Vv, Yo
Sputter	24 (0.10)	3	JJ, Ft, PO
Leaf clip	77 (0.32)	11	TA, FF, YL, PO, JJ, PE, Ka, Fn, Pm, Vl, Fl
Ant dip	7 (0.03)	4	TA, PO, Yo, Vv
Leaf for drink	7 (0.03)	5	TA, Ka, Fn, Pm, Fl
Nut crack	2 (0.01)	1[f]	PO
Pestle pound	2 (0.01)	3	PO, Ka, Ft
Stick to get honey	2 (0.01)	1	PO
Other tool use[g]	10 (0.04)	3	YL, PO, Ft

[a] Includes behavior of focal and non-focal individuals
[b] Numbers in parentheses indicate freq/hour. n=241 h of observation
[c] Males are shown in abbreviates with two capital letters; and females with a capital and a small letters
[d] Includes cases when only one party touched other's genitals (see also text)
[e] Includes both participants
[f] Performer was not identified in one case
[g] Club, throw object, play with object, etc

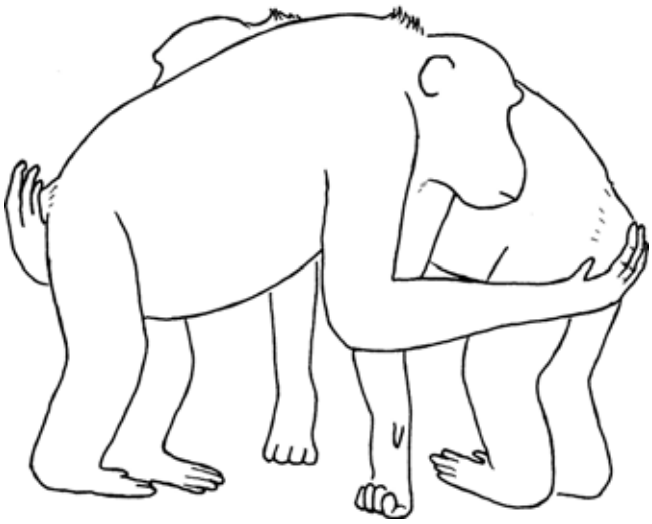

Fig. 1 Mutual genital touch by Bossou female chimpanzees (*Pan troglodytes*). Drawn from memory

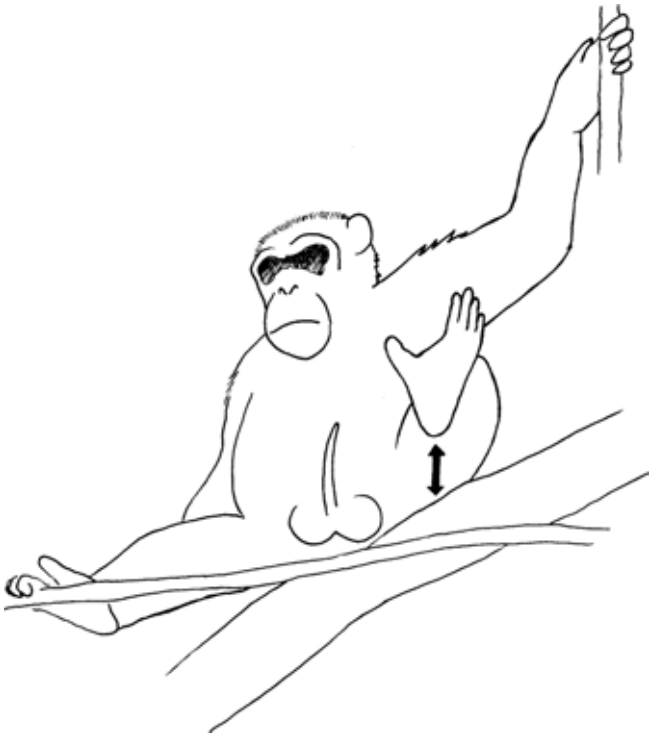

Fig. 2 Heel tap by a Bossou male. Drawn from video footage

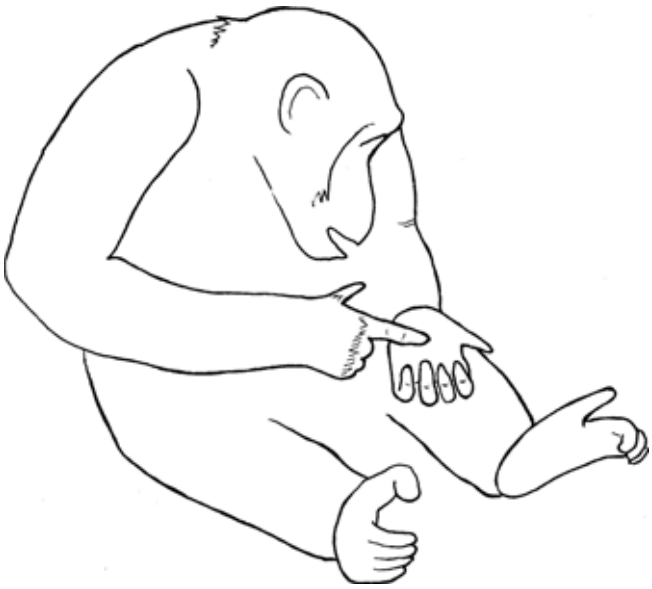

Fig. 3 Index to palm by a Bossou male. Drawn from video footage